



JAVIER KAYNAN TRINDADE

**FROM ASHES TO SPROUTS: *PRIMING* AND FIRE-INDUCED
SEED GERMINATION OF CAMPO RUPESTRE SPECIES**

**LAVRAS – MG
2025**

JAVIER KAYNAN TRINDADE

**FROM ASHES TO SPROUTS: *PRIMING* AND FIRE-INDUCED SEED GERMINATION
OF CAMPO RUPESTRE SPECIES**

Dissertation submitted to the Universidade Federal de Lavras as part of the requirements of the Graduate Program in the Master's Degree in Plant Physiology, with a concentration in Plant Growth and Development, for the attainment of the title of Master.

Advisor
Prof. DSc. Elisa Monteze Bicalho

**LAVRAS – MG
2025**

Ficha catalográfica elaborada pelo Sistema de Geração de Ficha Catalográfica da Biblioteca Universitária da UFLA, com dados informados pelo(a) próprio(a) autor(a).

Trindade, Javier Kaynan

From Ashes to Sprouts: Priming and Fire-Induced Seed Germination of Campo Rupestre Species / Javier Kaynan
Trindade - UFLA, 2025.

49 p. : il.

Dissertação (mestrado) – Universidade Federal de Lavras, 2024.

Orientadora: Elisa Monteze Bicalho.

Bibliografia.

1. Germinação . 2. Priming . 3. Campo rupestre . 4. Plântulas .
5. Bioquímica.

JAVIER KAYNAN TRINDADE

**DAS CINZAS AS BROTAÇÕES: *PRIMING* E GERMINAÇÃO DE SEMENTES
INDUZIDA PELO FOGO DE ESPÉCIES DO CAMPO RUPESTRE**

**FROM ASHES TO SPROUTS: PRIMING AND FIRE-INDUCED SEED GERMINATION
OF CAMPO RUPESTRE SPECIES**

Dissertation submitted to the Universidade Federal de Lavras as part of the requirements of the Graduate Program in the Master's Degree in Plant Physiology, with a concentration in Plant Growth and Development, for the attainment of the title of Master.

APPROVED on 21 de july, 2025.

DSc. Elisa Monteze Bicalho	UFV
DSc. Leandro Elias Morais	IFMG
DSc. Rosana Marta Kolb	UNESP

Advisor
Prof. DSc. Elisa Monteze Bicalho

**LAVRAS – MG
2025**

To my parents and my nephews, with love.

Dedicate.

ACKNOWLEDGMENTS

I thank my parents for their immense support, trust, and encouragement throughout this stage.

To my nephews, Helena and Luiz Felipe, whom I love dearly.

To my brother Adilson and my sister-in-law Ana Paula, for also being a source of support during this period.

To the part of my family residing in São Paulo, who have always cared for and supported me, my most sincere gratitude to them.

To my childhood friends, who, despite the distance and the demands of life, have always believed in me.

To the friends I made through UFLA and Plant Physiology (whose names I choose not to mention here to avoid the risk of forgetting someone, which would be unforgivable), all of you, in some way, have been part of my life over these past years. Your support was undoubtedly crucial for the completion of this work.

To my advisor, Elisa, who has guided me since my undergraduate years and has always inspired me with her sensitivity in observing nature. Thank you for the opportunity to learn, for your persistence, patience, and trust.

I would like to extend my gratitude to all the staff at UFLA, especially those responsible for the groundwork for the maintenance and operation of the spaces, without whom this work would not have been possible.

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

To FAPEMIG (Fundação de Amparo à Pesquisa do Estado de Minas Gerais), for funding this project under the Universal 2023 FAPEMIG call (Call 01/2023).

I would like to thank the Programa de Pós-graduação em Fisiologia Vegetal - PPGFV for all the support during this period of great challenge and learning.

Finally, I would like to thank the Universidade Federal de Lavras - UFLA, to which I owe my sincere thanks, for providing me with countless lessons and personal and professional growth over the last six years.

“Seja você quem for, seja qual for a posição social que você tenha na vida, a mais alta ou a mais baixa, tenha sempre como meta muita força, muita determinação e sempre faça tudo com muito amor, que um dia você chega lá. De alguma maneira você chega lá”

(Ayrton Senna)

RESUMO

O fogo é um distúrbio natural que integra as paisagens de ecossistemas abertos, como o Campo Rupestre (CR), onde as espécies, ao longo do tempo, se adaptaram e prosperaram em condições pós-fogo. Embora o fogo esteja presente nesse ambiente, seus efeitos fisiológicos sobre a dinâmica da vegetação ainda são pouco compreendidos. Sabe-se, no entanto, que ele desempenha um papel importante no recrutamento de plântulas a partir de sementes presentes no banco de sementes do solo, as quais podem passar por ciclos de hidratação e desidratação ao absorver moléculas químicas derivadas da queima da vegetação. Neste estudo, investigamos a técnica de priming de sementes com compostos da fumaça em sementes de *Vellozia compacta* e *Vellozia caruncularis*, simulando a passagem do fogo pelo banco de sementes. O experimento foi composto por sementes com e sem tratamento de priming com "água de fumaça", que foram enterradas em três simulações distintas de banco de sementes no solo: (1) controle, (2) cinzas oriundas da queima de vegetação do campo rupestre, e (3) passagem do fogo sobre vegetação do campo rupestre. Após os tratamentos, e dois dias de umidificação, as sementes foram exumadas para análises fisiológicas. Foram analisados parâmetros germinativos (percentual de germinação e índice de velocidade de germinação - IVG) e quantificados marcadores bioquímicos nas plântulas (açúcares solúveis totais, aminoácidos totais e malondialdeído - MDA). O priming com "água de fumaça" resultou em melhores parâmetros germinativos para ambas as espécies sob as condições de simulação do fogo (3). Em contraste, para os parâmetros bioquímicos nas plântulas, as concentrações de açúcares solúveis totais e de aminoácidos totais foram mais elevadas nas condições controle e de simulação com cinzas. Essa resposta foi mais acentuada com a aplicação do priming. O priming também foi relevante para a redução dos níveis de MDA, um composto formado pela peroxidação lipídica. Este estudo sugere que os efeitos fisiológicos e bioquímicos do priming com componentes químicos da fumaça em sementes de espécies de Velloziaceae do CR podem induzir uma memória fisiológica nas plantas durante a fase inicial de crescimento. Contudo, essa resposta é complexa, e estudos adicionais são necessários para compreender o papel do fogo na germinação e no recrutamento de plântulas.

Palavras-chave: Campo Rupestre; Fogo; Fumaça; Germinação; Plântulas; *Priming*.

ABSTRACT

Fire is a natural disturbance that integrates the landscapes of open ecosystems such as the Campo Rupestre (CR), where species have adapted and thrived in post-fire conditions over time. Although fire is present in this environment, its physiological effects on vegetation dynamics are still poorly understood. Still, it is known that it plays an important role in the recruitment of seedlings from seeds found in the soil seed bank, which can experience cycles of hydration and dehydration by absorbing chemical molecules derived from burning vegetation. Here, we investigated the technique of priming seeds with smoke compounds in seeds of *Vellozia compacta* and *Vellozia caruncularis* in a simulation of the passage of fire through the seed bank. The experiment was composed of primed or non-primed seeds with smoked water, which were buried in three different soil seed bank simulations: (1) control, (2) ashes from burned vegetation of campo rupestre, and (3) fire passage on vegetation of campo rupestre. After the treatments, two days of being unimified, the seeds were exhumed for physiological analysis. Germination parameters were analyzed (germination percentage, and germination speed index - GSI), and biochemical markers (total soluble sugars, total amino acids, and malondialdehyde - MDA) were quantified in the seedlings. Priming with “smoked water” showed better germination parameters in both species in the fire simulation conditions (3). In contrast, for the biochemical parameters in the seedlings, the amount of total soluble sugars and total amino acids was higher in the control conditions and under fire simulation with the ashes. This response was more stimulated with the application of priming. The priming was important for reducing the MDA levels, a compound formed by lipid peroxidation. This study suggests that the physiological and biochemical effects of priming with chemical components from smoke in seeds of Velloziaceae species of CR can generate a memory in plants in the initial growth phase. However, this response is complex, and further studies are needed to understand the role of fire in germination and seedling recruitment.

Keywords: Campo Rupestre; Fire; Smoke; Germination; Seedlings; *Priming*.

INDICADORES DE IMPACTO

A crescente degradação de áreas naturais, intensificada pela exploração antrópica, tem comprometido a biodiversidade e o equilíbrio ecológico de ecossistemas únicos como o Campo Rupestre. Nesse contexto, a restauração ambiental surge como uma necessidade urgente e estratégica, não apenas para conservar espécies nativas, mas também para fomentar benefícios sociais, econômicos e ecológicos mais amplos. Essa pesquisa, sobre os efeitos do fogo na germinação de sementes de duas espécies nativas (*Vellozia compacta* e *Vellozia caruncularis*) apresenta inovações que podem transformar práticas de revegetação em áreas impactadas e propensas ao fogo.

A utilização da técnica de *priming* em sementes com “água de fumaça” - solução obtida a partir da queima de material vegetal, mostrou-se promissora ao induzir maior germinação em sementes e melhor estabelecimento de plantas em crescimento inicial, conferindo maior tolerância de mudas em campo. Isso representa um avanço tecnológico relevante, pois integra um elemento típico do Campo Rupestre, o fogo em uma estratégia de baixo custo voltada à restauração ecológica.

O impacto social desse estudo se estende à promoção de práticas sustentáveis em diferentes setores. Empresas podem empregar áreas revegetadas para obtenção de créditos de carbono e certificações ambientais; iniciativas de pagamento por serviços ecossistêmicos (PSE) podem ser fortalecidas; e setores como o ecoturismo, o extrativismo sustentável e o mercado imobiliário também se beneficiam da valorização de áreas restauradas com espécies nativas. Adicionalmente, o desenvolvimento de protocolos para o uso da técnica com “água de fumaça” pode fomentar a comercialização de sementes mais resistentes, com maior viabilidade e potencial de armazenamento, agregando valor à cadeia produtiva de sementes e mudas nativas.

Do ponto de vista científico, a pesquisa é pioneira na análise dos mecanismos bioquímicos e fisiológicos envolvidos na ação dos compostos da fumaça sobre sementes e em plântulas das duas espécies estudadas. Os resultados oferecem subsídios para o uso do *priming* como ferramenta eficaz em programas de restauração ambiental, especialmente em ecossistemas propensos a queimadas naturais.

IMPACT INDICATORS

The increasing degradation of natural areas, intensified by anthropogenic exploitation, has compromised biodiversity and the ecological balance of unique ecosystems such as the Campo Rupestre. In this context, environmental restoration emerges as an urgent and strategic necessity not only to conserve native species, but also to foster broader social, economic, and ecological benefits. This research, which investigates the effects of fire on the seed germination of two native species (*Vellozia compacta* and *Vellozia caruncularis*), presents innovations that may transform revegetation practices in fire-prone and impacted areas.

The use of seed *priming* with “smoked water”, a solution derived from the combustion of plant material, has proven promising in promoting higher germination rates and better early plant establishment, enhancing the field tolerance of seedlings. This represents a significant technological advance, as it incorporates a characteristic element of the Campo Rupestre fire into a low-cost strategy aimed at ecological restoration.

The social impact of this study extends to the promotion of sustainable practices across various sectors. Companies can use revegetated areas to obtain carbon credits and environmental certifications; payment for ecosystem services (PES) initiatives can be strengthened; and sectors such as ecotourism, sustainable extractivism, and real estate can also benefit from the valorization of restored areas with native species. Additionally, developing protocols for the use of the smoke water technique may encourage the commercialization of more resilient seeds with greater viability and storage potential, adding value to the native seed and seedling supply chain.

From a scientific perspective, this research is pioneering in its analysis of the biochemical and physiological mechanisms involved in the action of smoked compounds on seeds and seedlings of the two studied species. The results provide a foundation for using *priming* as an effective tool in environmental restoration programs, especially in ecosystems prone to natural fires.

SUMMARY

1 INTRODUCTION	12
2 THEORETICAL FRAMEWORK.....	13
2.1 Fire and its consequences modulating plant growth and development	13
2.2 Campo Rupestre	14
2.3 Fire, smoke and seed germination.....	16
2.4 Seed <i>priming</i>	17
3 MATERIAL AND METHODS	19
3.1 Plant material.....	19
3.2 Smoked water procedures.....	19
3.3 <i>Priming</i> procedures: using the smoked water for imbibing the seeds.....	20
3.4 Experimental procedures: soil seed bank – fire and smoke effects simulation	21
3.5 Germination experiments and seedling sampling.....	22
3.6 Biochemical analyses	23
3.7 Experimental design and statistical analyses	24
4 RESULTS.....	24
4.1 Germination parameters.....	24
4.2 Biochemical parameters.....	26
5 DISCUSSION.....	28
6 FINAL CONSIDERATIONS	31
REFERENCES	33

1 INTRODUCTION

Campos Rupestres are a phytophysionomy of the Atlantic Forest, Cerrado, and Caatinga biomes (Miola et al. 2021), hosting approximately 5.000 species of vascular plants, which represents around 14% of Brazilian floristic biodiversity (Silveira et al. 2016). This remarkable diversity is associated with natural selection events and processes involving genetic drift (Rapini et al. 2021). However, anthropogenic and climatic changes are negative pressures that could lead to the loss of numerous endemic species in this environment. Fernandes et al. (2020), emphasize that open ecosystems, such as the Campos Rupestres, are often neglected in conservation and species maintenance efforts, which over time has facilitated resource exploitation in these phytophysionomies.

Naturally, the occurrence of fires in campo rupestre plays a significant role in the ecological and evolutionary processes over time, which have been shaping the configuration of this ecosystem (He, 2019; Oliveira et al. 2016). The passage of fire can lead to a high and rapid germination of some seeds present in the soil, representing an adaptive advantage for post-fire regeneration (Baskin & Baskin, 2014; Stradic et al., 2015a, b). However, the fire itself, i.e., burning and high temperature, it is not the only component of the environment modification, because ‘where there is fire, there is smoke’.

The resulting smoke from the combustion of plant materials contains various compounds that can promote plant growth and development, positively affecting certain species (Brown 1993; Van Staden 2006; Waters & Nelson, 2023). However, the modulation of vegetation by fire can be a problem when it is used uncontrolled, clandestinely, and periodically, damaging the re-establishment of local flora. Although many species of fauna and flora are resilient and adapted to this disturbance, it can hinder the establishment of new organisms and species that respond negatively to fire and smoke (Fernandes et al. 2019; Pausas, 2019; Silva et al. 2023; Zirondi et al. 2019). Thus, considering alternatives for the restoration of degraded areas prone to fire is fundamental for the safety and survival of many species, so pre-treating seeds with smoke-derived compounds can be an alternative to this problem (Hodges et al. 2021).

A strategy to overcome this problem is the use of seed *priming*, a technique in which orthodox seeds can be soaked in a specific solution until halfway through phase two of the three-phase pattern of water absorption, without germinating properly, and then dried to their original fresh weight (Farooq et al. 2006a, 2006b; Bradford, 1986). The germination process of orthodox seeds goes through three distinct physiological phases. Phase I is characterized by

rapid water absorption driven by the low water potential of the dry seed, resulting in an increase in fresh weight without significant metabolic activity; in phase II, water absorption stabilizes, but metabolic processes resume, such as cell repair, enzyme synthesis, respiratory activation and remobilization of reserves; finally, phase III marks the beginning of actual germination, signaled by the protrusion of the radicle and the start of seedling establishment (Nonogaki et al. 2010).

This dynamic of imbibing, and drying seeds in a controlled manner can intensify metabolic and biochemical adjustments during the germination and post-germination process (Paparella et al. 2015). This technique can provide several benefits to the seeds and, consequently, enhances seedling establishment by increasing vigor, uniformity, and overall germination rates (Farooq et al. 2019).

This work aimed to determine whether seeds previously treated with *priming* of smoke extract exhibit greater tolerance to a potential fire passage scenario in the vegetation, by simulating the seeds in the soil. The hypothesis addressed was: the seed *priming* of two *Vellozia* species with compounds derived from the burning of plant material improve seed germination, as well as benefit the seedlings with the biochemical memory induced in the seeds by *priming*.

2 THEORETICAL FRAMEWORK

2.1 Fire and its consequences modulating plant growth and development

Since the "boom" of plant emergence on Earth at the end of the Jurassic and the beginning of the Cretaceous, several events have shaped vegetation over time. Fires resulting from volcanic eruptions and storms, along with an increase in oxygen in the atmosphere, were quite intense during this period (Brown et al. 2012). However, many plants, especially the most derived group, the angiosperms, showed adaptations to coexist with fire and to exploit it to survive and maintain their descendants (Brown et al. 2012; Pausas and Lamont, 2022).

The discovery of chemical compounds from the burning of plant material in the 1990s, as potential plant regulators, spurred numerous studies to understand the behavior of fire and smoke in plant growth and development (De Lange and Boucher, 1990). Smoke resulting from the burning of plant material can contain more than 4.000 chemical components, which can trigger physiological responses in plants (Sakuma et al. 1981; Andreoli et al. 2003).

These numerous compounds can modulate different responses in plants, in the early growth phase, water containing smoke compounds can interact with some hormones, such as gibberellins, which can act synergistically to promote germination and seedling development. These compounds increase lipid peroxidation in the endosperm, mobilizing reserves and reducing oxidative stress by increasing the synthesis of antioxidant enzymes (Sunmonu et al. 2016; Yang et al. 2019). Another response is related to the mechanisms of perception of light quality, demonstrating that these chemical compounds in the signaling pathway promote the activity of transcription factors responsible for the response to light in plants, regulating the processes of photomorphogenesis (Bursch et al. 2021). In response to the photosynthetic process, these may be more efficient with the use of smoke compounds, favoring an increase in plant biomass and productivity even under adverse conditions (Komatsu et al., 2022; Shah et al., 2020; Sharifi e Bidabadi, 2020).

These responses from these chemists are important to think about in open environments, such as tropical savannas, where herbaceous vegetation is predominant, making up the main source of fuel for fires in these areas (Trollope, 1982; Veldman et al., 2015). Fire acts as a significant disturbance, inducing profound effects on ecosystems, causing the destruction of plants and, often, leading to short-, medium-, and long-term changes in the composition of plant communities (Bond and Van Wilgen, 1996; Trollope, 1982; Veldman et al., 2015; Bond and Keeley, 2005; Bond, 2004).

However, plants can regenerate after a fire through (i) resprouting (Pilon et al. 2020; Zupo et al. 2020); (ii) the breaking of seed dormancy in seeds buried in the soil (Pausas and Lamont 2022; Waters & Nelson, 2022), and (iii) by serotiny, when seeds are kept in cones or fruits for some time until they are released by an environmental stimulus, such as fire (Lamonte et al. 2020). The mechanism of promoting germination through fire varies; the heat generated by the passage of fire can cause the thick seed coat to crack, increasing its permeability to water, which leads to imbibition and subsequently germination. Another mechanism involves chemical compounds present in smoke, charcoal, or ash, which can stimulate better germination parameters and break the physiological dormancy of certain seeds (Brits, 1986; Cochrane et al. 2002; Flematti et al. 2013; Burrows, Alden, & Robinson, 2018; Moreira et al. 2010; Stradic et al. 2015).

2.2 Campo Rupestre

Campos Rupestres occur in the highest elevations of four major orographic systems: the Espinhaço Range, the Mantiqueira Range, Serra dos Carajás and the Serra do Mar. They are recognized as important centers of endemism for the neotropical flora (Giulietti & Pirani 1988, Eiten 1992, Giulietti et al. 1997, Safford 1999, Rapini et al. 2008, Fiaschi & Pirani 2009; Silva et al. 1996). Historically, Magalhães, 1966 and Joly, 1970 were pioneers in using the term “Campos Rupestres”, considering the vegetation, altitude, and soil composition in which species are distributed.

Currently, this environment is characterized as a complex vegetational ecosystem with rich plant diversity, occurring on nutrient-poor soils. It is predominantly composed of graminoid patches and shrubs, though it also includes woody species (Mucina, 2018; Neves et al. 2018). Messias et al. 2012, and Silveira et al. 2016, define it as a montane grassland with shrubby species adapted to fire, forming a mosaic of endemic vegetation associated with quartzitic, ferruginous, or sandstone rock outcrops, as well as sandy soils, stones, and seasonally flooded grasslands.

The formation of the floristic composition of this environment resulted from the long-term isolation of populations and species, facilitating speciation and leading to the highest rate of endemism among Brazil's vegetation types. Additionally, it exhibits a high species turnover across different locations (De Bano et al. 1995; Echternacht et al. 2011; Neves et al. 2018; Colli-Silva et al. 2019; Mattos et al. 2019). In Brazilian territory, this ecosystem covers only 0.8% of the surface area; however, it harbors 15% of the country's entire flora, making it the most critical biodiversity hotspot in the country (Silveira et al. 2016; Fernandes et al. 2014, 2018).

One of the botanical families that stands out in this ecosystem is the Velloziaceae, which has its center of diversity and endemism in the Campos Rupestres, whose species comprise a third of the vegetation cover of several communities (Mello-Silva et al. 2011; Zemunik et al. 2018). This family has herbaceous species with leaves arranged in rosettes and their roots are aerial (Ayensu, 1973; Demetrio, 2020), capable of dissolving quartzite rocks, releasing P, and contributing to the biological weathering of rocks (Porder, 2019; Teodoro et al. 2019). *Vellozia caruncularis* Mart. ex Seub. and *Vellozia compacta* Mart. ex Schult. & Schult.f. are endemic species which make up a rich diversity of rocky grasslands and have suffered from the increasingly frequent anthropogenic impacts on these areas.

Recognized as a megadiverse ecosystem, Campo Rupestre is currently threatened by anthropogenic exploitation of both fauna and flora (Fernandes, 2016; Fernandes et al. 2018). Some issues, such as fire regimes resulting from human action, have impacted the Campos

Rupestres, modifying their floristic composition (Drummond et al. 2018). Although the vegetation is resilient and adapted to the passage of fire, as is the case with species of the Velloziaceae family (Alves et al. 2010; Souza et al. 2018), the periodicity of burning events can promote initial competitive advantages for non-native plants, as fire can cause an increase in the availability of nutrients, favoring the emergence of these plants (Coutinho, 1990; Nardoto et al. 2006). However, more research is needed to assess the impact of fire on the dynamics of the Campo Rupestre vegetation (Silveira et al. 2016).

Silveira et al. (2016), highlight the need for conservation efforts regarding the Campo Rupestre, as it is an ancient ecosystem, considered both a museum of ancient lineages and a cradle of diversification for endemic lineages. Therefore, immediate measures are necessary to mitigate anthropogenic threats that could lead to further losses in this ecosystem over the coming decades (Fernandes et al. 2020). Furthermore, given the lack of literature on the morphological characterization and propagation of many of these species, it is essential to advance their understanding to support habitat regeneration, revegetation, and the maintenance of ecological communities.

2.3 Fire, smoke and seed germination

Seed germination represents a delicate and critical phase in the plant life cycle, influenced by both intrinsic seed traits and external environmental conditions (Bewley et al., 2013). Fire events can significantly alter these conditions, often promoting the germination of a greater number of species from the seed bank. This highlights both the direct and indirect effects of fire on seed germination and subsequent seedling recruitment (Dairel and Fidelis, 2024).

The molecules present in smoke can induce biochemical responses in seeds. Several studies have demonstrated mechanisms of action of compounds extracted from smoke that mimic and/or suppress the effect of red light on light-sensitive seeds. This process is based on the conversion of phytochrome from its inactive form to its active form, in addition to interacting with gibberellins, the main hormone involved in inducing germination (Panda et al. 2022; Wang et al. 2022). Therefore, it is likely that smoke affects membrane permeability or red-light receptor sensitivity to induce germination responses (Brown and Van Staden, 1997; Gupta et al. 2019; Jamil et al. 2020; Van Staden et al. 1995).

When dispersed, seeds may encounter atypical conditions for germination (Pandey et al. 2025). Khatoon et al. (2020) demonstrated the role of smoke derived from plants in the morphological, physiological, and biochemical mechanisms of plant growth under stress conditions. Jamil et al. (2014) found that treating seeds with plant-derived smoke enhanced germination and seedling growth under saline stress by improving ion balance, increasing chlorophyll, carotenoids, nitrogen, and total protein levels. Already Shah et al. (2022), showed that under water stress, smoke-derived compounds enhance antioxidant enzyme activity and elevate organic and amino acid levels in seedlings, reducing oxidative damage and supporting redox homeostasis.

These adverse conditions, such as low water availability, high salt content in the soil and high temperatures to which seeds and seedlings are subjected, can cause oxidative damage due to the accumulation of reactive oxygen species (ROS) in the system, impairing growth and development (Bhattacharjee, 2012; Choudhary et al., 2020; Mhamdi and Van Breusegem, 2018). In wheat, smoke derived compounds from plants act by eliminating the ROS, increasing antioxidant enzyme activity, stimulating the expression of stress-responsive genes, and increasing proline content, an important osmoprotectant that enhances plant tolerance to stress (Shabir et al. 2020; Küçükakyüz and Çatav, 2021; Iqbal et al. 2018).

Another effect of smoke compounds is their interaction with hormones such as cytokinins, gibberellins, abscisic acid and ethylene. Smoke can act by sensitizing the embryo to these hormones, increasing the embryo's sensitivity to them, so that the levels of endogenous hormones, which are normally too low to trigger germination, become active/promoting (Van Staden et al. 2008).

2.4 Seed *priming*

One of the first scientists around the world to verify the priming effects in seeds was the naturalist and evolutionary biologist Charles Darwin (1809–1882), who subjected the seeds to immersion in seawater to enhance germination, thus inducing osmopriming (Darwin, 1855 a, b; Paparella et al. 2015). The priming technique, which Darwin already used, aims to hydrate/imbibe and dry seeds in a controlled manner before sowing, allowing the metabolic processes of germination to proceed without actual germination (Farooq et al. 2006). The three-phase soaking pattern of orthodox seeds is essential for understanding the methodology and mechanisms of priming. In the first phase, there is a large increase in the seed's fresh

weight due to the rapid absorption of water, followed by the stabilization of fresh weight in phase two, when metabolic processes are reactivated and reserves are remobilized, culminating in the last phase, marked by germination (Nonogaki et al. 2010).

Seeds treated with priming show greater and more uniform germination due to enzyme activation, cell repair mechanisms, protein synthesis and antioxidant defense mechanisms, when compared to untreated seeds, and this response also extends to the biochemical parameters of the seedlings during their establishment (Dias et al. 2024; Orunsolu et al. 2025; Silva et al. 2023).

Priming also increases the accumulation of osmolytes, such as proline, glycine betaine, and polyamines, through alterations in metabolic processes that can confer greater tolerance to seeds and seedlings (Afzal et al. 2008; Delavari et al. 2010; Jafar et al. 2012; Marthandan et al. 2020). This method also has the potential to improve plant adaptation, enhancing tolerance to both biotic and abiotic stresses (Khalaki et al. 2021).

Plants may face various stresses throughout their development, and studies show that plants from seeds treated with priming techniques have greater tolerance to stresses, in general (Hussain et al. 2018; Ibrahim, 2016; Nedunchezhiyana et al. 2020; Ofoe et al. 2022). Thus, different preparation techniques (hydro, osmo, chemical, physical, and biostimulants) are applied to increase tolerance to abiotic stresses, such as saline or drought stress (Johnson et al. 2021).

In *hydropriming* treatment, seeds are soaked in water under optimal temperature conditions, being considered the most well-known *priming* method, though it is currently applied compared to other methods (Johnson et al. 2021; Taylor et al. 1998). Osmopriming is a widely used procedure that involves treatment with osmotic solutions at low water potential, facilitating the control of water absorption and ensuring successful germination of many species (Marthandan et al. 2020). Chemical treatments with substances like hormones can directly impact seed metabolism, being effective in developing stress tolerance (Moori et al. 2020; Nouri and Haddioui 2021).

However, the use of *priming* with chemical smoke compounds in mitigating biotic and abiotic stresses is scarce in the literature, making the knowledge of smoke's action as a priming effect unknown. However, studies report that smoke-derived compounds, considered plant regulators, such as karrikins, have positive effects during plant growth and development (Khatoon et al. 2020).

3 MATERIAL AND METHODS

3.1 Plant material

The plant material was collected in March of 2024, in the Parque Estadual da Serra do Rola-Moça, in the municipality of Nova Lima, Minas Gerais. Seeds of *Vellozia caruncularis* Mart. ex Seub. and *Vellozia compacta* Mart. ex Schult. & Schult.f. (20°03'38.9"S, 44°02'01.3"W) were collected from at least ten individual mother plants. After collecting the fruit, the seeds were processed by hand and stored in paper bags for 10 months at 5°C until the start of the experiments. In addition to the seeds, the litter layer was also collected (20°03'14.4"S, 44°00'07.7"W) from the same environment to extract the "smoked water".

3.2 Smoked water procedures

For the extraction of "smoked water", an adaptation of the methodology described by Akeel et al. (2019) (Fig. 1), was carried out, utilizing two Kitasato flask, one containing the burnt litter layer and the other receiving the smoke compounds, a vacuum pump, and a heater (± 280 -300°C). The proportion of litter layer to water was 5g to 50 mL, as described by Fernandes et al. (2020). At the end of extraction, 50 ml of the "smoked water" was produced in the Kitasato flask coupled to a vacuum pump. This process yielded a stock solution, and the pH of the solution was measured. In all extractions, the pH was approximately 3.8.

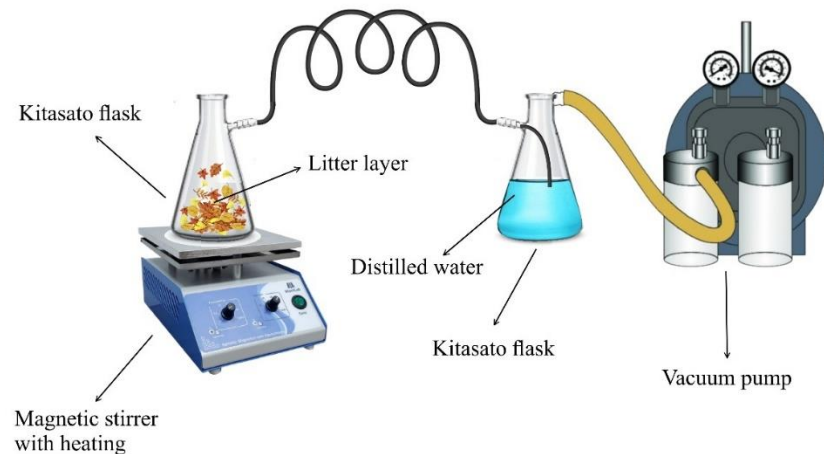


Figure 1: Smoke water extraction procedure. There were used two KITASATO flask; one is puted above the heater containing the litter layer that is interconnected with other kitasato flask containing distilled water and one vacuum pump that received the smoked water from the first kitasato flask.

3.3 Priming procedures: using the smoked water for imbibing the seeds

For the *priming* procedures, the seed imbibition and drying curves were defined. For all species, an imbibition curve was established (increase in fresh weight along with the imbibition time), followed by a drying curve (decrease in fresh weight until the initial mass is reached), to determine the appropriate time for *priming*. To carry out the imbibition curve, five replicates were used for each species, containing 0.1g of seeds in each replicate; these seeds were imbibed in distilled water and placed in Petri dishes, being weighed every hour until germination was visualized (2mm radicle).

The time to reach the phase II of imbibition curve were 48h. Next, for the drying curve, five repetitions were also used for each species, where they were placed on germination paper and disposed in gerboxes containing silica gel. The gerboxes were kept at a controlled temperature of 25°C in a germination chamber, and the seeds were weighing every hour until they reached dry weight (initial weight, before starting imbibition).

Seeds of each species were disposed in microtubes containing a 1:10 dilution of the stock smoked water solution for the priming procedure. The seeds stayed 48h imbibing in 1:10 smoked water, dried for 4 hours at a controlled temperature of 25 °C, and then used in the experiments. Non-primed seeds were used as another source of variation of seeds pre-treatment.

3.4 Experimental procedures: soil seed bank – fire and smoke effects simulation

The experiments were set to simulate the fire passage or smoked dilution compounds in water when seeds are buried in soil seed banks. Three metal trays measuring 30 × 40 cm and 6 cm high, perforated to drain the water, were used. A total of 9 kg of red clay type soil, in a 2:1 ratio of soil to sand, was added to each tray. *Unpriming* (seeds that have not undergone priming) and *SWpriming* (primed seeds with smoked water – SW) The seeds were placed in metal mesh envelopes 1 cm above the soil surface, then covered with a further 4 cm of soil. Each envelope contained 500 seeds of *V. compacta* or *V. caruncularis*.

Each tray represented a different condition. In the first treatment (control), the trays containing the seeds received only water, without litter layer. In the second treatment (ashes), ashes from previously burned plant material were applied on the top of the substrate of the trays, followed by water. In the last treatment (fire), the plant material - 3 cm high containing 0.275 kg of Campo Rupestre litter layer - was placed on the tray and burned on top of the soil, simulating the passage of the fire, which burned for about 10 minutes. At the end of combustion, the soil was thoroughly moistened to maintain field capacity for seed imbibition. The fire treatment contained a digital thermometer where the seed envelopes were, to record the temperature during the fire. The temperature before the fire was 27.2°C (for all trays) and during the burning, the maximum temperature was 51.0°C (Fig. 2).

The volume of water applied was determined using a Haines funnel (Cássaro et al. 2008) to estimate the field capacity concerning the soil proportion. The seeds of both species remained in the soil seed bank for a period defined by the imbibition curve, 48 hours for both *V. compacta* and *V. caruncularis*. After this period, the envelopes containing the seeds were exhumed, and germination tests were conducted.

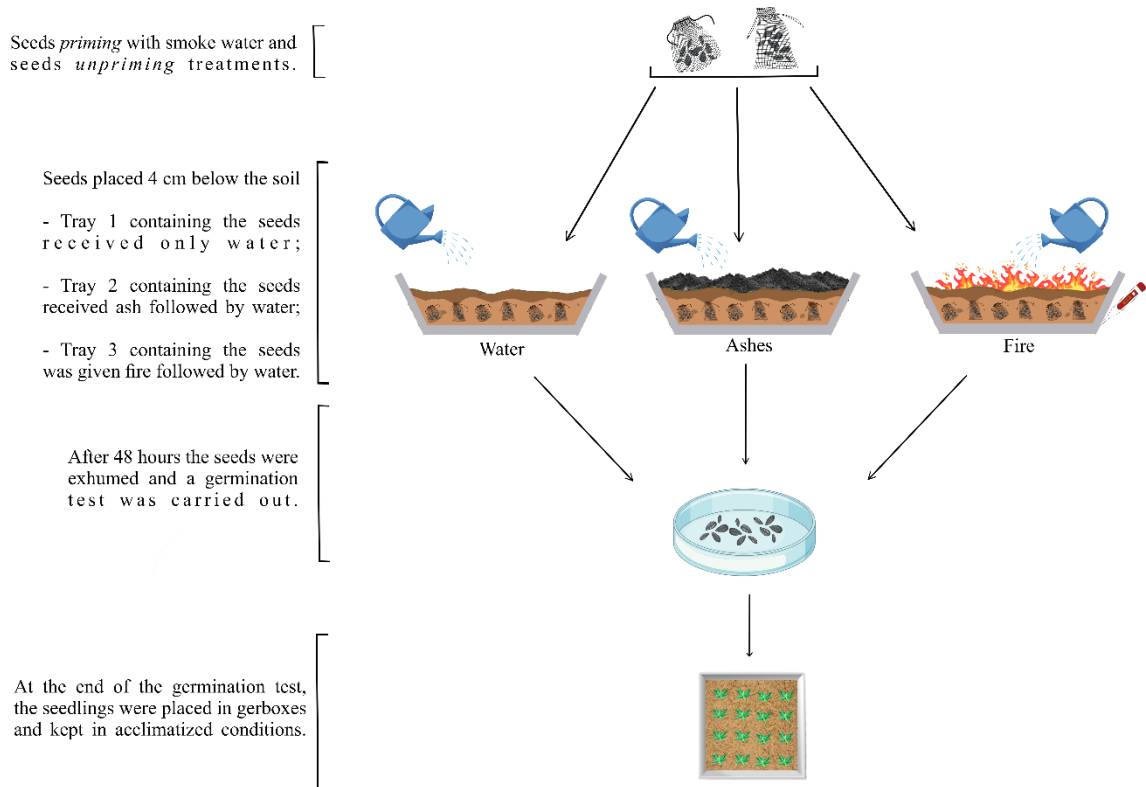


Figure 2: Simulation of soil seed bank scheme in tree trays: seeds of the *Vellozia compacta* and *Vellozia caruncularis* with *unpriming* and *priming* with smoke water (*SWpriming*) were set in packs and distributed in tree trays, simulating different conditions. In the first one, the seeds received only water, simulating the control; in the second tray ashes from the burned the vegetal material were used; and in the third tray there was the simulation of the passage of the fire. All the trays, were watered and kept hydrated for 48 hours until exhumation of the seeds, and assembly of the germination test. In the end of the germination test, all the seedling were transported to gerbox with a sand bed for seedling establishment.

3.5 Germination experiments and seedling sampling

Before the germination tests, all seeds were disinfected with 1.5% sodium hypochlorite for 10 minutes, followed by rinsing in distilled water three times. The germination tests for the *Vellozia* species were carried out in germination boxes using two layers of germination paper, and the seeds were placed in germination chambers with a photoperiod of 12 hours of light with $40 \mu\text{M}$ of photons $\text{m}^{-2} \text{s}^{-1}$, at the optimal temperature for each species: 25°C for *V. caruncularis* (Vieira et al. 2018) and 30°C for *V. compacta* (Bicalho et al. 2017). For the germination tests, the germination percentage, germination speed index (GSI) (Maguire, 1962), and cumulative germination were calculated by daily counting the number of germinated seeds and the total number germinated at the end of the experiment, considering the radicle protrusion.

At the end of the germination experiment, the seedlings were transferred to germination boxes containing autoclaved sand and maintained under laboratory conditions for two months for acclimatization, until collection for biochemical analyses. The seedling presented that 2-3 leaves (Fig. 3-A, B) when were sampled. The samples were macerated in liquid nitrogen and weighed for later extraction and quantification of biochemical markers.

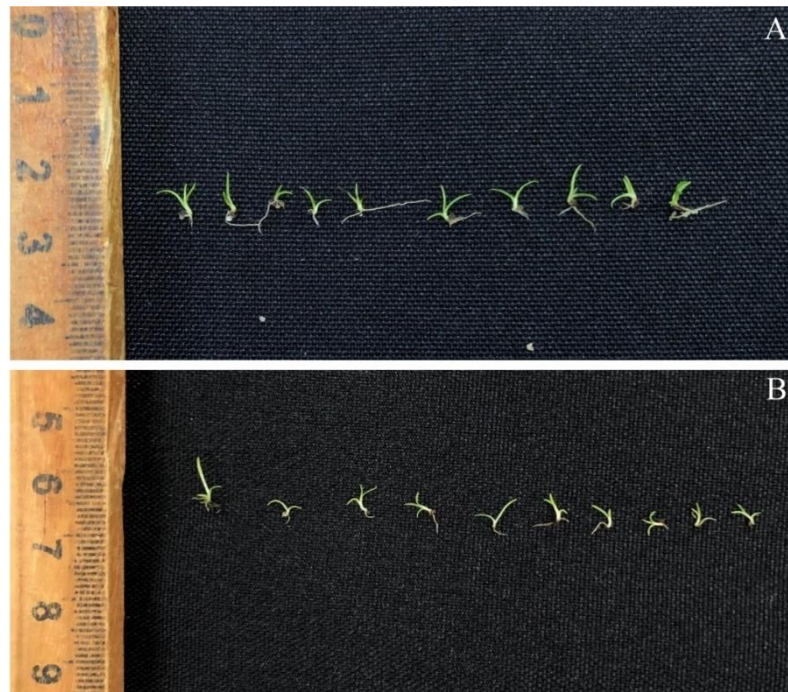


Figure 3: Seedling of the *Vellozia compacta* (A) and *Vellozia caruncularis* (B) before the collected to biochemistry analysis.

3.6 Biochemical analyses

The extraction followed a protocol from López-Hidalgo (2020), using a sequential ethanolic extraction (100%, 80%, and 50% ethanol). Each ethanolic extract was centrifuged for 10 minutes at 4 °C, then subjected to a water bath at 70–75 °C for 20 minutes. After each extraction step, the supernatant was collected and combined into a single tube for subsequent quantification of the biochemical markers. Free amino acids (FAA) (Yemm and Cocking, 1955), malondialdehyde (MDA) (Buege and Aust, 1978), and total soluble sugars (TSS) (Yemm and Willis, 1954) were measured, as follows.

For quantifying the TSS, 40mg of the anthrone, 1 mL of distilled water and then add 20 mL of sulfuric acid were mixed. For the standard curve, we used increased concentrations of glucose and, 1 mL of the anthrone solution was added in each tube. These tubes were

transferred to a bath at 100°C for 5 minutes and read at 620 nm on a spectrophotometer. The amount of TSS was calculated according to the standard curve.

For the FAA quantifying, it was prepared on reagent mix with sodium citrate buffer (0,25 mL), ninhydrin (0,1 mL) and potassium cyanide (0,5 mL). For the standard curve was utilized crescent concentrations of glycine, 850 µL of the reagent mix and 650 µL of the ethanol 60%. These tubes were transfer to the bath at 100°C for 5 minutes and read at 570 nm of absorbance. The amount of FAA was calculated according to the standard curve.

For the MDA, was used one aliquot of the 125 µL of the sample was pipetted in one microtube with 250 µL that reaction medium that trichloroacetic acid (0,5%) and thiobarbituric acid (10%) and later, these microtubes with samples were transfer to the bath at 95°C for 30 minutes. Each sample was in duplicated thus, 2 tubes were used per sample. After the time in the bath, the reaction was stopped in ice following pipetted that 200 µL of the sample and read absorbances at 535 and 600 nm. The extension of lipid peroxidation was calculated by $[MDA] = (A_{535} - A_{600}) / (\epsilon X b)$, in which ϵ = molar extinction coefficient = $1,56 \times 10^{-5}$, b = optical length = 1.

3.7 Experimental design and statistical analyses

The experiments were in randomized design in two-way scheme, with two seeds treatments (*unpriming* and *SWpriming*) and tree different conditions (control, soil with ashes and fire) where the seeds were buried. For each metal tray, there were used four packs with *unpriming* seed and 4 packs with *SWpriming* seed; for each specie; in each pack there were 500 seeds, which were used for germination tests. For the biochemistry analysis, there were used all the seedlings formed along with germination test. The seedlings were macerated and weighty between 0,02 – 0,08 mg to compose each repetition.

Statistical analyses were carried out using R studio software. The data were subjected to the Shapiro-Wilk normality test, analysis of variance and Tukey's test at 5% probability.

4 RESULTS

4.1 Germination parameters

In general, *Vellozia sp.* seeds subjected to *SWpriming* increased germination parameters compared to seeds not subjected to *SWpriming*. In *V. compacta*, the conditions of the water, ashes and fire, did not impacted the percentage of germination and GSI (Fig. 4-A, C). However, the treatments with *SWpriming* presented high germinative parameters comparing with *unpriming* seed (Fig. 4-A, C). This difference was clearly observed in cumulative germination curve, where the seed *SWpriming* stood out with greater speed and germination percentage (Fig. 4-E).

Regarding to *V. caruncularis*, the conditions of the water, ashes and fire impacted the germination of this specie, in germination percentage and GSI (Fig. 4-B, D, F). The seeds kept under ‘fire’ condition showed increased germination in relation to those from ‘control’ or from ‘ashes’, independent of being or not primed (Fig. 4-B). The *SWpriming* induced faster germination in all conditions; but *unprimed* seeds increased germination only in ‘fire’ conditions, in relation to ‘control’ or to ‘ashes’ (Fig. 5-D).

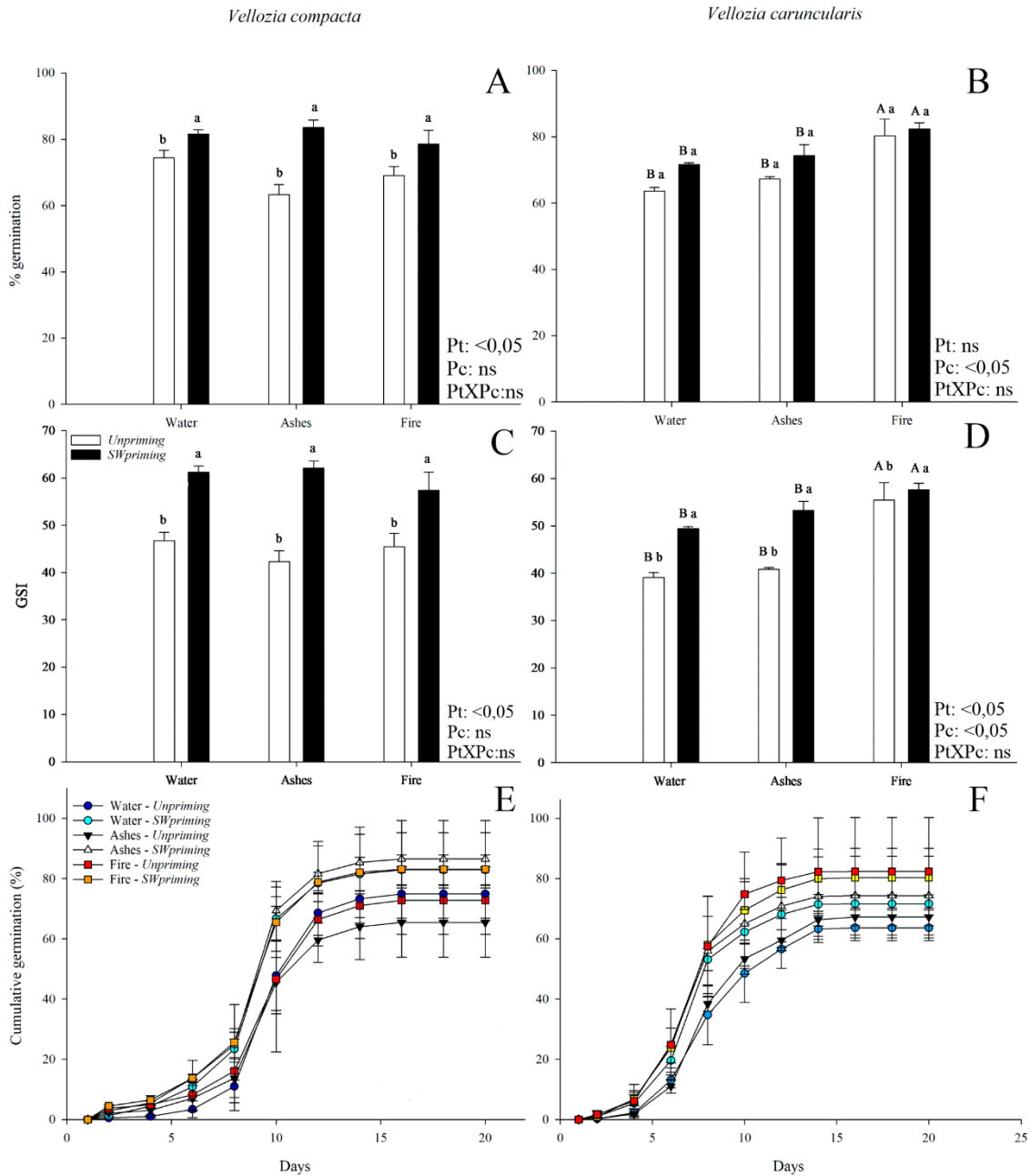


Figure 4: Germination percentagem; germination speed index (GSI) and acumulative germination of the *Vellozia compacta* and *Vellozia caruncularis* species with *SWpriming* treatments (black bars) and *unpriming* (white bars) under different conditions: water, ashes and fire. Significant differences ($p < 0,05$) between *priming* treatments are marked with lower case letters, while for the diferente conditions, upper case letters. Pt, P-value between treatments; Pc, P-value between conditions; PtXPc, P-value the interaction of treatments and conditions; Ns (not significant) do not show any significant difference by Tukey’s test at 5% significance. Data are means \pm standard errors ($n = 4$).

4.2 Biochemical parameters

Seed treatment and the conditions they were kept during soil seed bank simulation impacted the levels of TSS, FAA and MDA in both species (Fig. 5). In *V. compacta*, there

was no difference in TSS between the *SWpriming* and *unpriming* treatments, but when comparing with the condition containing ashes, showed a higher amount of sugars compared to control and fire (Fig. 5-A).

SWpriming treatment promoted the highest amount of FAA under the condition where the seed bank received only ashes, while for *unpriming*, the increased values of FAA were found in the condition where the seeds received only water (Fig. 5-C). The lowest values of FAA were found in the condition where fire was applied, independent of the priming treatment. MDA was lower in all treatments of seedlings generated from *SWpriming* seeds, but there was no statistical difference between the conditions water, ashes and fire (Fig. 5-E).

In *V. caruncularis*, the levels of TSS were influenced both by priming treatment and conditions where the seeds were kept. The seedlings from *SWpriming* treatment stood out in the conditions where the seeds were exposed to water and ashes in the seed bank, while for *unpriming*, the seedlings showed the highest accumulation of TSS in the tray that received only water (Fig. 5-B). Comparing the best conditions for TSS accumulation in seedlings, the condition water in the seedlings from ‘water’ condition, independent of pre-treatment, and *SWpriming* from ‘ashes’ condition experienced the highest values of TSS accumulation (Fig. 5-B).

Similarly to TSS, the ‘fire’ conditions induced reductions in concentration of FAA, independently of the seeds pretreatment. In water condition, seedlings from *unpriming* accumulated increased levels of FAA, while in ‘ashes’ condition seedling from *SWpriming* showed the highest levels (Fig. 5-D). In terms of MDA accumulation, *SWpriming* in the tree different conditions presented decreased accumulation of the MDA comparing the *unpriming* seeds, however, comparing that water, ashes and fire, there was no statistical difference between them. (Fig. 5-F).

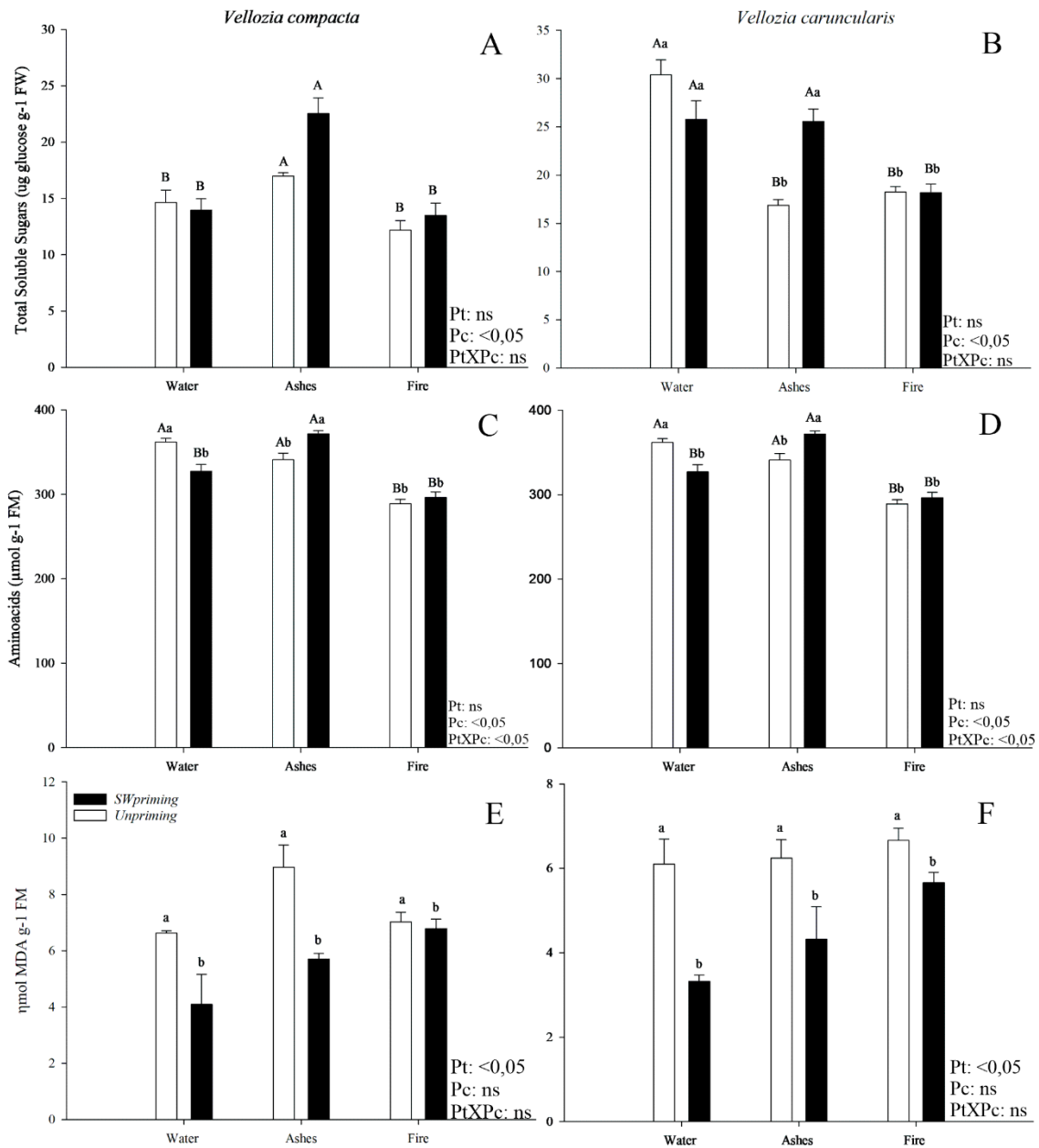


Figure 5: Total Soluble Sugars (TSS); Aminoacids (FAA) and Malondialdehyde (MDA) of the *Vellozia compacta* and *Vellozia caruncularis* specie with *SWpriming* treatments (black bars) and *unpriming* (white bars) under different conditions: water, ashes and fire. Significant differences ($p < 0,05$) between *priming* treatments are marked with lower case letters, while for the diferente conditions, upper case letters. Pt, P-value between treatments; Pc, P-value between conditions; PtXPc, P-value between the interaction of treatments and conditions. Ns (not significant) do not show any significant difference by Tukey's test at 5% significance. Data are means \pm standard errors ($n = 3$).

5 DISCUSSION

This work brings, for the first time, the fire and ashes effects on germination and seedling biochemical changes of Velloziaceae seeds treated or not with smoked water. It was

possible to verify that seeds pretreatment influences seed germination in distinct ways in both species studied, as well as in the seedlings sampled, according to the conditions where the seeds were kept after pretreatments. In *V. caruncularis*, fire induced higher germination parameters, acting as an environmental cue to promote germination at optimal times for survival and ecosystem regeneration. This effect was enhanced by the application of *priming*. In contrast, *V. compacta* did not show changes in germination parameters due to fire, but rather in response to *priming*. Fire provides nature-based cues to trigger germination in many taxa, both in fire-prone and non-fire-prone habitats worldwide (Soós et al. 2019). Heat shocks caused by flames (Aguayo-Villalba et al. 2021; Dairel & Fidelis, 2020; Zironi et al., 2019) and chemical signals from smoke (Nelson et al. 2012; Pandey et al. 2024; Ramos et al. 2019; Staden et al. 2000) are the most frequently reported fire-related effects that promote seed germination and seedling establishment.

Despite the two *Vellozia* species studied here showing different responses to fire simulation in terms of germination, both responded similarly to the *priming* treatment, indicating that seeds of these species may be stimulated as they absorb these compounds in a post-fire scenario, reflecting on the speed of germination. In Campos Rupestres, species from the Velloziaceae family can form long-term seed banks upon seed dispersal (Garcia et al. 2017), and these seed banks are modulated across seasons until a suitable germination window arises, allowing the seedling recruitment. It is known that most seed dispersal in Campo Rupestre occurs before spring, with peak of germination occurring during the rainy season (Garcia et al. 2020). However, the imbibition process may not occur continuously in some seeds, which then experience hydration-dehydration (HD) cycles (Meiado, 2013; Dias et al. 2024).

Seeds of Velloziaceae family from Campo Rupestre do not show physiological dormancy, but they are dependent of light to germinate (Garcia et al. 2020). Because of this, they can form long-term soil seed banks (Garcia et al. 2017), in which the recurrent imbibition and drying cause the priming effect. In this work, both species studied were benefited to *priming* application, increasing both germination percentage and velocity, the crucial effects of priming on seeds (Paparella et al. 2015). Besides improving germinability, seed priming with smoked water could induced signaling to seedling recruitment in both *Vellozia* species studied here. The smoked water or pyrolysis products have been used for inducing seed germination in fire-prone species (Keeley and Pausas, 2018; Alahakoon et al. 2020). The joint action of thousand compounds can result in additive, synergistic or antagonistic effects on germination (Bose et al. 2020; Gupta et al. 2019). The seed *priming* treatments can also

improve ‘priming memory’ in seedlings (Lutts et al. 2016), as some biochemical results seen in this work.

In *V. compacta* and *V. caruncularis*, the results show that alterations in sugar metabolism, increasing the level of this, triggered by smoke water *priming* were crucial for plant growth and development during the initial stages. Pre-treatments with smoke-derived compounds significantly influence sucrose metabolism, triggering increased enzymatic activity such as that of sucrose synthase and enhancing total soluble sugar content (Rehman et al. 2018). Some works indicate that smoke can affect the activity of sucrose-cleaving enzymes, which play important roles in regulating plant growth and development (Koch, 2004; Sturm and Tang, 1999). Glucose signaling mediated by invertases may induce the expression of genes involved in cell division and auxin biosynthesis, directly influencing plant growth (LeClere et al. 2010; Ruan, 2012).

Both species exhibited a higher accumulation of free amino acids in seedlings subjected to treatments simulating the chemical effects of fire through ash application and under control conditions. This suggests that smoke-derived compounds can markedly alter total protein and amino acid contents (Aremu et al. 2012, 2014; Singh et al. 2014). Rehman et al. (2018) presented proteomic analyses revealing that proteins related to branched-chain amino acid metabolism may be affected. This greater accumulation of free amino acids may be explained by intensified protein degradation, possibly through protein ubiquitination processes and activation of genes related to proteolysis (Chyliński et al. 2007; Soós et al. 2010).

In the *Vellozias* sp. studied here, *priming* with smoke-derived compounds increased free amino acid levels, which is directly associated with improvements in germination parameters and seedling growth. It is well-established in the literature that seed *priming* can induce various biochemical modulations, improving seedling establishment (Anwar et al. 2020; Louis et al. 2023). This is likely due to enhanced enzyme activity, such as amylase and sucrose synthase, which intensifies the mobilization of stored reserves, including proteins that are broken down into free amino acids (Singh et al. 2024; Wang et al. 2022). Under adverse conditions, the increase in free amino acids such as proline contributes to osmotic adjustment, enhancing plant tolerance to stress and being accompanied by heightened antioxidant activity (Rao et al. 2023; Zhang et al. 2015).

In the species studied here, a higher accumulation of MDA was observed in seedlings derived from untreated seeds, in contrast to those subjected to *priming*. Various environmental factors can induce stress conditions, impairing growth and development, but

priming can reduce oxidative damage during the germination process and seedling establishment (Ghiyasi et al. 2024; Goswami et al. 2013; Jisha and Puthur, 2016; Ren et al. 2023; Salah et al. 2015). Additionally, smoke-derived compounds may also act by enhancing the efficiency of the antioxidant system, leading to lower MDA accumulation in plant tissues (Ağci et al. 2024; Gupta et al. 2022; Pinit et al. 2023). Reduced lipid peroxidation and oxidative stress damages were also seen after *priming* treatments in other species (Orunsolu et al. 2025; Pereira et al. 2022; Silva et al. 2023).

Between species, *V. caruncularis* showed to maintain the ‘*priming* memory’ even in seedlings, however, this effect seems to be lost when the seeds were in ‘fire’ condition. In *V. caruncularis* seedlings, the reductions in sugars and aminoacids due to fire passage when the seeds were buried might be related to increasing temperature (51 °C), that probably stimulated the reserves consumption. Interestingly, the germination percentage and velocity of *V. caruncularis* seeds increased due to fire in relation to the ‘water’ and ‘ashes’. It seems that this species, which occurs in fire-prone environments, improves germinability after the passage of fire, more because of the temperature than the compounds in the smoke, which has already been reported by Vieira et al. (2017). Otherwise, *V. compacta* seedlings seem not to be sensible to keep priming memory, but its effects were very pronounced on seed germination, independent of the condition they were kept after priming. For *V. compacta*, it seems that the seeds are very sensible to HD, but not necessarily to fire passage and increasing temperature.

This study demonstrates that the two native species investigated are capable of responding to fire-related cues, highlighting their potential resilience in fire-prone environments. The use of smoke-derived compounds in seed *priming* proved to be a promising strategy for enhancing germination and promoting better seedling establishment, suggesting its applicability in revegetation and ecological restoration. Furthermore, this research presents for the first time how seed germination and seedling establishment of *V. compacta* and *V. caruncularis* are modulated by fire occurrence, and how seeds treated with smoke-compound priming respond to these modulations, offering physiological and ecological insights into the persistence of these species in their natural environment.

6 FINAL CONSIDERATIONS

This study brings significant contributions about the fire acting in seed bank soil and seedling establishment, as well as investigating *priming* in seeds after the passage of the fire in two important species from Velloziaceae family from Campo Rupestre.

The fire passage and the post-fire conditions can inducing directly signal in the seed bank soil through the action physical and chemistry. These signals were observed in the dynamic of the germination of the *Vellozias* sp. with the increase in germination parameters, highlighting the adaptive value of these species to fire. The responses of this condition to germination are adjusted to the specific thresholds of each species, the environmental triggers, and the intrinsic physiological factors of the seeds.

The seed *priming* technique, can be an important procedure to better germinative parameter and induce better biochemical responses during seedling establishment. Here, the two species pre-treated with “smoke water” *priming* (*SWpriming*) showed better germination parameters and this response was extended during their initial growth. Thus, *SWpriming* could be an alternative for promoting restoration via direct seeding of fire-prone areas, at least for Campo Rupestre.

These responses reaffirm the ecological importance of fire as a disturbance and a regenerative force intertwined with the various strategies of native vegetation. Thus, understanding this dynamic is essential for conservation and rewilding processes, as well as predicting the resilience of plant communities in the face of altered fire regimes due to climate change or anthropogenic pressures. This is a pioneering study in understanding the biochemical factors of *V. compacta* and *V. caruncularis* seedlings after fire. Future ecological, physiological and biochemical research should be carried out to better understand the resilience of native Campo Rupestre vegetation in the face of fire episodes.

REFERENCES

- ABBASI KHALAKI, Masoomah et al. Influence of nano-priming on seed germination and plant growth of forage and medicinal plants. **Plant growth regulation**, v. 93, n. 1, p. 13-28, 2021.
- ABREU, Marcel Carvalho et al. Temporal and spatial patterns of fire activity in three biomes of Brazil. **Science of the Total Environment**, v. 844, p. 157138, 2022.
- AFZAL, I. et al. Halopriming improves vigor, metabolism of reserves and ionic contents in wheat seedlings under salt stress. **Plant Soil Environ**, v. 54, n. 9, p. 382-388, 2008.
- AKEEL, Arshiya et al. Smoke-saturated water and karrikinolide modulate germination, growth, photosynthesis and nutritional values of carrot (*Daucus carota* L.). **Journal of Plant Growth Regulation**, v. 38, n. 4, p. 1387-1401, 2019.
- ALAHAKOON, A. A. C. B. et al. Species-specific smoke effects on seed germination of plants from different habitats from Sri Lanka. **Flora**, v. 263, p. 151530, 2020.
- ALCANTARA, Berenice K. et al. Soluble amino acid profile, mineral nutrient and carbohydrate content of maize kernels harvested from plants submitted to ascorbic acid seed priming. **Anais da Academia Brasileira de Ciências**, v. 89, n. 1 suppl, p. 695-704, 2017.
- ALVES, Ruy José Válka; KOLBEK, Jiří. Vegetation strategy of *Vellozia crinita* (Velloziaceae). **Biologia**, v. 65, n. 2, p. 254-264, 2010.
- ANDREOLI, Cristina; GIGANTE, Daniela; NUNZIATA, Alfredo. A review of in vitro methods to assess the biological activity of tobacco smoke with the aim of reducing the toxicity of smoke. **Toxicology in vitro**, v. 17, n. 5-6, p. 587-594, 2003.
- ANWAR, Ali; XIANCHANG, Y. U.; YANSU, L. I. Seed priming as a promising technique to improve growth, chlorophyll, photosynthesis and nutrient contents in cucumber seedlings. **Notulae Botanicae Horti Agrobotanici Cluj-Napoca**, v. 48, n. 1, p. 116-127, 2020.
- AREMU, Adeyemi O. et al. Stimulatory role of smoke–water and karrikinolide on the photosynthetic pigment and phenolic contents of micropropagated ‘Williams’ bananas. **Plant growth regulation**, v. 67, p. 271-279, 2012.

AREMU, Adeyemi O.; MASONDO, Nqobile A.; VAN STADEN, Johannes. Smoke–water stimulates secondary metabolites during in vitro seedling development in *Tulbaghia* species. **South African Journal of Botany**, v. 91, p. 49-52, 2014.

AYENSU, Edward S. Biological and morphological aspects of the Velloziaceae. **Biotropica**, p. 135-149, 1973.

BAILLY, Christophe et al. Antioxidant systems in sunflower (*Helianthus annuus* L.) seeds as affected by priming. **Seed Science Research**, v. 10, n. 1, p. 35-42, 2000.

BASKIN, Carol C.; BASKIN, Jerry M. (Ed.). **Plant regeneration from seeds: a global warming perspective**. Academic Press, 2022.

BERINGER, Jason et al. Fire in Australian savannas: from leaf to landscape. **Global change biology**, v. 21, n. 1, p. 62-81, 2015.

BHATTACHARJEE, Soumen. The language of reactive oxygen species signaling in plants. **Journal of Botany**, v. 2012, n. 1, p. 985298, 2012.

BICALHO, Elisa Monteze; SOARES-DA-MOTA, Leticia A.; GARCIA, Queila Souza. Temperature and light requirements for germination of species of Velloziaceae from different Brazilian rocky outcrops. **Acta Botanica Brasilica**, v. 32, p. 240-246, 2018.

BOSE, Utpal et al. Multi-omics strategies for decoding smoke-assisted germination pathways and seed vigour. **International Journal of Molecular Sciences**, v. 21, n. 20, p. 7512, 2020.

BOWMAN, David MJS et al. The human dimension of fire regimes on Earth. **Journal of biogeography**, v. 38, n. 12, p. 2223-2236, 2011.

BRADFORD, Kent J. Manipulation of seed water relations via osmotic priming to improve germination under stress. **HortScience**, v. 21, n. 5, p. 1105-1112, 1986.

BRITS, G. J. Influence of fluctuating temperatures and H₂O₂ treatment on germination of *Leucospermum cordifolium* and *Serruina florida* (Proteaceae) seeds. **South African Journal of Botany**, v. 52, n. 4, p. 286-290, 1986.

BROWN, Neville AC; VAN STADEN, Johannes. Smoke as a germination cue: a review. **Plant growth regulation**, v. 22, n. 2, p. 115-124, 1997.

BROWN, Sarah AE et al. Cretaceous wildfires and their impact on the Earth system. **Cretaceous research**, v. 36, p. 162-190, 2012.

BROWNE, F. L. 1958. Theories of the combustion of wood and its control. Report Number 2136 (Information reviewed and reaffirmed 1963). USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin.

BURROWS, Geoffrey E.; ALDEN, Rowan; ROBINSON, Wayne A. The lens in focus—lens structure in seeds of 51 Australian Acacia species and its implications for imbibition and germination. **Australian Journal of Botany**, v. 66, n. 5, p. 398-413, 2018.

BURSCH, Katharina et al. Karrikins control seedling photomorphogenesis and anthocyanin biosynthesis through a HY5-BBX transcriptional module. **The Plant Journal**, v. 107, n. 5, p. 1346-1362, 2021.

CALHEIROS, T.; PEREIRA, M. G.; NUNES, João Pedro. Assessing impacts of future climate change on extreme fire weather and pyro-regions in Iberian Peninsula. **Science of The Total Environment**, v. 754, p. 142233, 2021.

CÁSSARO, Fabio Augusto Meira et al. Funil de Haines modificado: curvas de retenção de solos próximos à saturação. **Revista Brasileira de Ciência do solo**, v. 32, p. 2555-2562, 2008.

CHERGUI, Brahim et al. Socioeconomic factors drive fire-regime variability in the Mediterranean Basin. **Ecosystems**, v. 21, p. 619-628, 2018.

CHOUDHARY, A.; KUMAR, A.; KAUR, N. ROS and oxidative burst: roots in plant development. *Plant Divers* 42: 33–43 [em linha]. 2020.

CHYLIŃSKI, Wojciech Karol; ŁUKASZEWSKA, Aleksandra Józefina; KUTNIK, Katarzyna. Drought response of two bedding plants. **Acta Physiologiae Plantarum**, v. 29, p. 399-406, 2007.

COCHRANE, Mark A.; LAURANCE, William F. Fire as a large-scale edge effect in Amazonian forests. **Journal of Tropical Ecology**, v. 18, n. 3, p. 311-325, 2002.

COLLINS, Luke et al. The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. **Environmental Research Letters**, v. 16, n. 4, p. 044029, 2021.

COLLI-SILVA, Matheus; VASCONCELOS, Thais NC; PIRANI, José Rubens. Outstanding plant endemism levels strongly support the recognition of campo rupestre provinces in mountaintops of eastern South America. **Journal of Biogeography**, v. 46, n. 8, p. 1723-1733, 2019.

COUTINHO, Leopoldo Magno. Fire in the ecology of the Brazilian cerrado. In: **Fire in the tropical biota: ecosystem processes and global challenges**. Berlin, Heidelberg: Springer Berlin Heidelberg, 1990. p. 82-105.

DA SILVA DIAS, G. et al. Be prepared: how does discontinuous hydration in *Tabebuia heterophylla* seeds induce stress tolerance in seedlings?. **Plant Biology**, 2024.

DA SILVA JUNIOR, Carlos Antonio et al. Persistent fire foci in all biomes undermine the Paris Agreement in Brazil. **Scientific Reports**, v. 10, n. 1, p. 16246, 2020.

DA SILVA JÚNIOR, Luiz Augusto Siciliano et al. Fire dynamics in extreme climatic events in western amazon. **Environmental Development**, v. 32, p. 100450, 2019.

DAIREL, Mariana; FIDELIS, Alessandra. Fire stimulates seedling recruitment from the seed bank in the Cerrado. **Journal of Vegetation Science**, v. 35, n. 3, p. e13268, 2024.

DARWIN, Charles (1855a) Effect of salt-water on the germination of seeds. *Gardeners' Chronicle and Agricultural Gazette* 47:773.

DARWIN, Charles (1855b) Does Sea water kill seeds? *Gardeners' Chronicle and Agricultural Gazette* 15 and 21 242:356–357.

DE ASSIS BARROS, Luizmar et al. Fire in the Atlantic Rainforest: an analysis of 20 years of fire foci distribution and their social-ecological drivers. **Geocarto International**, v. 37, n. 16, p. 4737-4761, 2022.

DE LANGE, Johannes H.; BOUCHER, C. Autecological studies on *Audouinia capitata* (Bruniaceae). I. Plant-derived smoke as a seed germination cue. **South African Journal of Botany**, v. 56, n. 6, p. 700-703, 1990.

DE MATTOS, Jacqueline Salvi et al. Plant phylogenetic diversity of tropical mountaintop rocky grasslands: local and regional constraints. **Plant Ecology**, v. 220, n. 12, p. 1119-1129, 2019.

DE OLIVEIRA DRUMMOND, Leandro; RODRIGUES MOURA, FILIPE; SILVERIO PIRES, Maria Rita. Impact of fire on anurans of rupestrian grasslands (campos rupestres): a case study in the Serra do Espinhaço, Brazil. **Salamandra**, v. 54, n. 1, 2018.

DE OLIVEIRA-JUNIOR, Jose Francisco et al. Fire foci related to rainfall and biomes of the state of Mato Grosso do Sul, Brazil. **Agricultural and Forest Meteorology**, v. 282, p. 107861, 2020.

DEBANO, Leonard H. et al. Biodiversity and management of the madrean archipelago: the sky islands of southwestern United States and northwestern Mexico. **Gen. Tech. Rep. RM-GTR-264. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 669 p.**, v. 264, 1995.

DEFOREST SAFFORD, Hugh. Brazilian Páramos I. An introduction to the physical environment and vegetation of the campos de altitude. **Journal of Biogeography**, v. 26, n. 4, p. 693-712, 1999.

DEMETRIO, Guilherme Ramos; BARBOSA, Mario Eduardo Avelar; DE FREITAS COELHO, Flávia. Plant density influence on life history traits of a perennial herb in rocky outcrops, southeastern Brazil. **Iheringia, Série Botânica.**, v. 75, 2020.

ECHTERNACHT, Livia et al. Areas of endemism in the Espinhaço range in Minas Gerais, Brazil. **Flora-Morphology, Distribution, Functional Ecology of Plants**, v. 206, n. 9, p. 782-791, 2011.

Ehrlén, J. & Eriksson, O. (2008) **Seedling recruitment and population ecology** *Ecology*, **76**, 239 - 254.

EITEN, George. Natural Brazilian vegetation types and their causes. **Anais da Academia brasileira de Ciências**, v. 64, n. 1, p. 35-66, 1992.

EVENARI, Michael. Seed physiology: its history from antiquity to the beginning of the 20th century. **The Botanical Review**, v. 50, p. 119-142, 1984.

EW, YEMM; AJ, WILLIS. The estimation of carbohydrates in plant extracts by anthrone. **The Biochemical Journal**, v. 57, n. 3, p. 508-514, 1954.

FAROOQ, Muhammad et al. Seed priming in field crops: potential benefits, adoption and challenges. **Crop and Pasture Science**, v. 70, n. 9, p. 731-771, 2019.

FAROOQ, Muhammad; BARSA, Shahzad MA; WAHID, Abdul. Priming of field-sown rice seed enhances germination, seedling establishment, allometry and yield. **Plant growth regulation**, v. 49, n. 2, p. 285-294, 2006.

FAROOQ, Muhammad; TABASSUM, R.; AFZAL, I. Enhancing the performance of direct seeded fine rice by seed priming. **Plant Production Science**, v. 9, n. 4, p. 446-456, 2006.

FERNANDES, Alessandra Furtado et al. The effect of fire on seed germination of campo rupestre species in the South American Cerrado. **Plant Ecology**, v. 222, n. 1, p. 45-55, 2021.

FERNANDES, G. Wilson et al. Floristic and functional identity of rupestrian grasslands as a subsidy for environmental restoration and policy. **Ecological Complexity**, v. 43, p. 100833, 2020.

FERNANDES, G. Wilson et al. The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. **Biodiversity and Conservation**, v. 27, p. 2587-2603, 2018.

FERNANDES, Geraldo Wilson et al. (Ed.). **Ecology and conservation of mountaintop grasslands in Brazil**. Switzerland: Springer International Publishing, 2016.

FERNANDES, Geraldo Wilson et al. Challenges for the conservation of vanishing megadiverse rupestrian grasslands. **Natureza & Conservação**, v. 12, n. 2, p. 162-165, 2014.

FIASCHI, Pedro; PIRANI, Jose R. Review of plant biogeographic studies in Brazil. **Journal of systematics and evolution**, v. 47, n. 5, p. 477-496, 2009.

FIDELIS, Alessandra; ZIRONDI, Heloiza L. And after fire, the Cerrado flowers: a review of post-fire flowering in a tropical savanna. **Flora**, v. 280, p. 151849, 2021.

FLANNIGAN, Michael D.; STOCKS, Brian J.; WOTTON, B. Mike. Climate change and forest fires. **Science of the total environment**, v. 262, n. 3, p. 221-229, 2000.

FLEMATTI, Gavin R. et al. Karrikin and cyanohydrin smoke signals provide clues to new endogenous plant signaling compounds. **Molecular Plant**, v. 6, n. 1, p. 29-37, 2013.

FREITAS, W. K. et al. Influence of fire foci on forest cover in the Atlantic Forest in Rio de Janeiro, Brazil. **Ecological Indicators**, v. 115, p. 106340, 2020.

GARCIA, Queila S. et al. Long-term persistence of Velloziaceae species in the soil seed bank in campo rupestre vegetation, Brazil. **Plant Ecology & Diversity**, v. 10, n. 4, p. 323-328, 2017.

GHIYASI, Mahdi et al. Machine learning insights into ascorbic acid-enhanced germination of black cumin (*Nigella sativa* L.) under cadmium stress. **Journal of Plant Growth Regulation**, p. 1-16, 2024.

GIULIETTI, Ana Maria; PIRANI, José Rubens. Patterns of geographic distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia. In: **Proceedings**. 1987.

GIULIETTI, Ana Maria; PIRANI, José Rubens; HARLEY, Raymond M. Espinhaço range region eastern Brazil. **Centres of plant diversity: a guide and strategy for their conservation**, 1997.

GOIS, Givanildo de; FREITAS, Wellington Kiffer de; OLIVEIRA JÚNIOR, José Francisco de. Spatial-temporal of fire foci in the state of Rio de Janeiro, Brazil. **Biosci. j.(Online)**, p. 1008-1017, 2020.

GOSWAMI, Alakananda; BANERJEE, Rahul; RAHA, Sanghamitra. Drought resistance in rice seedlings conferred by seed priming: role of the anti-oxidant defense mechanisms. **Protoplasma**, v. 250, p. 1115-1129, 2013.

GUERRA, Angélica et al. Drivers and projections of vegetation loss in the Pantanal and surrounding ecosystems. **Land Use Policy**, v. 91, p. 104388, 2020.

GUPTA, N. K. et al. On-farm hydro and nutri-priming increases yield of rainfed pearl millet through physio-biochemical adjustments and anti-oxidative defense mechanism. **Plos one**, v. 17, n. 6, p. e0265325, 2022.

GUPTA, Shubhpriya et al. Role of smoke stimulatory and inhibitory biomolecules in phytochrome-regulated seed germination of *Lactuca sativa*. **Plant physiology**, v. 181, n. 2, p. 458-470, 2019.

HARDESTY, Jeff; MYERS, Ron; FULKS, Wendy. Fire, ecosystems, and people: a preliminary assessment of fire as a global conservation issue. In: **The George Wright Forum**. George Wright Society, 2005. p. 78-87.

HARVEY, Brian J.; DONATO, Daniel C.; TURNER, Monica G. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. **Global Ecology and Biogeography**, v. 25, n. 6, p. 655-669, 2016.

HE, Tianhua; LAMONT, Byron B.; PAUSAS, Juli G. Fire as a key driver of Earth's biodiversity. **Biological Reviews**, v. 94, n. 6, p. 1983-2010, 2019.

HODGES, Joshua A. et al. Smoke and heat can increase germination of common wildflowers and grasses—implications for conservation and restoration of critically endangered grassy ecosystems. **Ecological Management & Restoration**, v. 23, n. 1, p. 94-99, 2022.

HUSSAIN, Mubshar et al. Mitigating the adverse effects of drought stress through seed priming and seed quality on wheat (*Triticum aestivum* L.) productivity. **Pakistan Journal of Agricultural Sciences**, v. 55, n. 2, 2018.

IBRAHIM, Ehab A. Seed priming to alleviate salinity stress in germinating seeds. **Journal of plant physiology**, v. 192, p. 38-46, 2016.

IQBAL, Muhammad et al. Smoke produced from plants waste material elicits growth of wheat (*Triticum aestivum* L.) by improving morphological, physiological and biochemical activity. **Biotechnology reports**, v. 17, p. 35-44, 2018.

JAFAR, M. Z. et al. Improving the performance of wheat by seed priming under saline conditions. **Journal of Agronomy and Crop Science**, v. 198, n. 1, p. 38-45, 2012.

JAMIL, Muhammad et al. Effect of plant-derived smoke priming on physiological and biochemical characteristics of rice under salt stress condition. **Australian Journal of Crop Science**, v. 8, n. 2, p. 159-170, 2014.

JAMIL, Muhammad; JAHANGIR, Muhammad; REHMAN, Shafiq Ur. Smoke induced physiological, biochemical and molecular changes in germinating rice seeds. **Pak. J. Bot**, v. 52, n. 3, p. 865-871, 2020.

JISHA, K. C.; PUTHUR, Jos T. Seed priming with BABA (β -amino butyric acid): a cost-effective method of abiotic stress tolerance in *Vigna radiata* (L.) Wilczek. **Protoplasma**, v. 253, p. 277-289, 2016.

JOHNSON, Riya; PUTHUR, Jos T. Seed priming as a cost-effective technique for developing plants with cross tolerance to salinity stress. **Plant physiology and biochemistry**, v. 162, p. 247-257, 2021.

JOLY, Aylthon Brandão. **Conheça a vegetação brasileira**. Editôra Polígono, 1970.

KEELEY, J. E.; PAUSAS, J. G. Evolution of 'smoke'induced seed germination in pyroendemic plants. **South African Journal of Botany**, v. 115, p. 251-255, 2018.

KEELEY, Jon E.; FOTHERINGHAM, C. J. Smoke-induced seed germination in California chaparral. **Ecology**, v. 79, n. 7, p. 2320-2336, 1998.

KEMP, Kerry B.; HIGUERA, Philip E.; MORGAN, Penelope. Fire legacies impact conifer regeneration across environmental gradients in the US northern Rockies. **Landscape Ecology**, v. 31, p. 619-636, 2016.

KHATOON, Amana et al. Plant-derived smoke affects biochemical mechanism on plant growth and seed germination. **International Journal of Molecular Sciences**, v. 21, n. 20, p. 7760, 2020.

KOCH, Karen. Sucrose metabolism: regulatory mechanisms and pivotal roles in sugar sensing and plant development. **Current opinion in plant biology**, v. 7, n. 3, p. 235-246, 2004.

KOLLER, Dov; KOZLOWSKI, T. T. Environmental control of seed germination. **Seed biology**, v. 2, p. 1-101, 1972.

KÜÇÜKAKYÜZ, Köksal; ÇATAV, Şükrü Serter. Physiological effects of smoke-water and karrikinolide on wheat seedlings grown under boron stress. **Russian Journal of Plant Physiology**, v. 68, n. 3, p. 552-558, 2021.

KULKARNI, Manoj G.; ASCOUGH, Glendon D.; VAN STADEN, Johannes. Smoke-water and a smoke-isolated butenolide improve growth and yield of tomatoes under greenhouse conditions. **HortTechnology**, v. 18, n. 3, p. 449-454, 2008.

LAMONT, Byron B. et al. Fire as a selective agent for both serotiny and nonserotiny over space and time. **Critical Reviews in Plant Sciences**, v. 39, n. 2, p. 140-172, 2020.

Law, L., & Xue, B. (2023). Internal cues for optimizing reproduction in a varying environment. *Proceedings of the Royal Society B: Biological Sciences*, 290.

LE STRADIC, Soizig et al. Diversity of germination strategies and seed dormancy in herbaceous species of campo rupestre grasslands. **Austral Ecology**, v. 40, n. 5, p. 537-546, 2015.

LE STRADIC, Soizig et al. Regeneration after fire in campo rupestre: Short-and long-term vegetation dynamics. **Flora**, v. 238, p. 191-200, 2018.

LEAL FILHO, Walter et al. Fire in Paradise: Why the Pantanal is burning. **Environmental Science & Policy**, v. 123, p. 31-34, 2021.

LECLERE, Sherry; SCHMELZ, Eric A.; CHOUREY, Prem S. Sugar levels regulate tryptophan-dependent auxin biosynthesis in developing maize kernels. **Plant Physiology**, v. 153, n. 1, p. 306-318, 2010.

LOBERT, J. M.; WARNATZ, J. Emissions from the combustion process in vegetation. **Fire in the Environment**, v. 13, p. 15-37, 1993.

LÓPEZ-HIDALGO, Cristina et al. **The rainbow protocol: A sequential method for quantifying pigments, sugars, free amino acids, phenolics, flavonoids and MDA from a small amount of sample**. Chichester, UK: John Wiley & Sons, Ltd., 2021.

LOUIS, Noble; DHANKHER, Om Parkash; PUTHUR, Jos T. Seed priming can enhance and retain stress tolerance in ensuing generations by inducing epigenetic changes and trans-generational memory. **Physiologia Plantarum**, v. 175, n. 2, p. e13881, 2023.

MAGALHÃES, G. M. Sobre os cerrados de Minas Gerais. **Anais da Academia Brasileira de Ciências**, v. 38, p. 59-70, 1966.

MAGALHÃES, Iara Barbosa et al. Brazilian Cerrado and Soy moratorium: Effects on biome preservation and consequences on grain production. **Land use policy**, v. 99, p. 105030, 2020.

MAGUIRE, James D. Speed of germination-aid in selection and evaluation for seedling emergence and vigor. 1962.

MAKHAYE, Gugulethu et al. Influence of plant biostimulant application on seed germination. Biostimulants for crops from seed germination to plant development, p. 109-135, 2021.

MARTHANDAN, Vishvanathan et al. Seed priming: a feasible strategy to enhance drought tolerance in crop plants. **International journal of molecular sciences**, v. 21, n. 21, p. 8258, 2020.

MELLO-SILVA, Renato et al. Five vicarious genera from Gondwana: the Velloziaceae as shown by molecules and morphology. **Annals of botany**, v. 108, n. 1, p. 87-102, 2011.

MESSIAS, Maria Cristina Teixeira Braga et al. Fitossociologia de campos rupestres quartzíticos e ferruginosos no Quadrilátero Ferrífero, Minas Gerais. **Acta Botanica Brasilica**, v. 26, p. 230-242, 2012.

MHAMDI, Amna; VAN BREUSEGEM, Frank. Reactive oxygen species in plant development. **Development**, v. 145, n. 15, p. dev164376, 2018.

MILLER, Russell G. et al. Experimental seed sowing reveals seedling recruitment vulnerability to unseasonal fire. **Ecological Applications**, v. 31, n. 7, p. e02411, 2021.

MIOLA, Deise TB; RAMOS, Vladimir DV; SILVEIRA, Fernando AO. A brief history of research in campo rupestre: identifying research priorities and revisiting the geographical distribution of an ancient, widespread Neotropical biome. **Biological Journal of the Linnean Society**, v. 133, n. 2, p. 464-480, 2021.

MOORI, Saeed; AHMADI-LAHIJANI, Mohammad J. Hormopriming instigates defense mechanisms in Thyme (*Thymus vulgaris* L.) seeds under cadmium stress. **Journal of Applied Research on Medicinal and Aromatic Plants**, v. 19, p. 100268, 2020.

MORALES, Melanie; MUNNÉ-BOSCH, Sergi. Malondialdehyde: facts and artifacts. **Plant physiology**, v. 180, n. 3, p. 1246-1250, 2019.

- MOREIRA, Bruno et al. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. **Annals of botany**, v. 105, n. 4, p. 627-635, 2010.
- MUCINA, Ladislav. Vegetation of Brazilian campos rupestres on siliceous substrates and their global analogues. **Flora**, v. 238, p. 11-23, 2018.
- NARDOTO, Gabriela Bielefeld et al. Nutrient use efficiency at ecosystem and species level in savanna areas of Central Brazil and impacts of fire. **Journal of Tropical Ecology**, v. 22, n. 2, p. 191-201, 2006.
- NEDUNCHEZHIAN, Vinothini; VELUSAMY, Manonmani; SUBBURAMU, Karthikeyan. Seed priming to mitigate the impact of elevated carbon dioxide associated temperature stress on germination in rice (*Oryza sativa* L.). **Archives of Agronomy and Soil Science**, v. 66, n. 1, p. 83-95, 2020.
- NEVES, Danilo M. et al. Lack of floristic identity in campos rupestres—A hyperdiverse mosaic of rocky montane savannas in South America. **Flora**, v. 238, p. 24-31, 2018.
- NONOGAKI, Hiroyuki; BASSEL, George W.; BEWLEY, J. Derek. Germination—still a mystery. **Plant science**, v. 179, n. 6, p. 574-581, 2010.
- NOURI, Mohamed; HADDIOUI, Abdelmajid. Improving seed germination and seedling growth of *Lepidium sativum* with different priming methods under arsenic stress. **Acta Ecologica Sinica**, v. 41, n. 1, p. 64-71, 2021.
- OFOE, Raphael et al. Seed priming with pyroligneous acid mitigates aluminum stress, and promotes tomato seed germination and seedling growth. **Plant Stress**, v. 4, p. 100083, 2022.
- OLIVEIRA, Rafael S. et al. Ecophysiology of campos rupestres plants. In: **Ecology and conservation of mountaintop grasslands in Brazil**. Cham: Springer International Publishing, 2016. p. 227-272.
- ORUNSOLU, Ibrahim Olajide et al. Halopriming as a tool for maintaining the vigor of sunflower seeds post storage. **Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology**, p. 1-7, 2025.

ORUNSOLU, Ibrahim Olajide et al. Halopriming as a tool for maintaining the vigor of sunflower seeds post storage. **Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology**, p. 1-7, 2025.

PANDA, Darshan et al. The role of phytochrome-mediated gibberellic acid signaling in the modulation of seed germination under low light stress in rice (*O. sativa* L.). **Physiology and Molecular Biology of Plants**, v. 28, n. 3, p. 585-605, 2022.

PANDEY, Nidhi et al. Smoke–water treatment of seeds, an ancient technique for increasing seed vigor. **Protoplasma**, v. 262, n. 1, p. 3-13, 2025.

PAPARELLA, S. et al. Seed priming: state of the art and new perspectives. **Plant cell reports**, v. 34, p. 1281-1293, 2015.

PAUSAS, Juli G.; LAMONT, Byron B. Fire-released seed dormancy-a global synthesis. **Biological Reviews**, v. 97, n. 4, p. 1612-1639, 2022.

PEREIRA, Aline Aparecida Silva et al. Can priming with ascorbic acid or nitric oxide improve the germinability of stored sunflower seeds?. **Journal of Seed Science**, v. 44, p. e202244012, 2022.

PILON, Natashi AL et al. The diversity of post-fire regeneration strategies in the cerrado ground layer. **Journal of Ecology**, v. 109, n. 1, p. 154-166, 2021.

PINIT, Sompop; ARIYAKULKIAT, Lalichat; CHAIWANON, Juthamas. Rice straw-derived smoke water promotes rice root growth under phosphorus deficiency by modulating oxidative stress and photosynthetic gene expression. **Scientific Reports**, v. 13, n. 1, p. 14802, 2023.,

PIVELLO, Vânia R. et al. Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. **Perspectives in Ecology and Conservation**, v. 19, n. 3, p. 233-255, 2021.

Porder, S. (2019). How plants enhance weathering and how weathering is important to plants. *Elements: An International Magazine of Mineralogy, Geochemistry, and Petrology*, 15(4), 241-246.

- RAO, Deepak et al. Silicic and Humic Acid Priming Improves Micro-and Macronutrient Uptake, Salinity Stress Tolerance, Seed Quality, and Physio-Biochemical Parameters in Lentil (*Lens culinaris* spp. *culinaris*). **Plants**, v. 12, n. 20, p. 3539, 2023.
- RAPINI, ALESSANDRO et al. A flora dos campos rupestres da Cadeia do Espinhaço. **Megadiversidade**, v. 4, n. 1-2, p. 16-24, 2008.
- REHMAN, Ali et al. Proteomic analysis of the promotive effect of plant-derived smoke on plant growth of chickpea. **Journal of Proteomics**, v. 176, p. 56-70, 2018.
- REN, Muyao et al. Priming methods affected deterioration speed of primed rice seeds by regulating reactive oxygen species accumulation, seed respiration and starch degradation. **Frontiers in Plant Science**, v. 14, p. 1267103, 2023.
- RUAN, Yong-Ling. Signaling role of sucrose metabolism in development. **Molecular plant**, v. 5, n. 4, p. 763-765, 2012.
- SAKUMA, Hirohiko; MUNAKATA, Sachiko; SUGAWARA, Shiro. Volatile products of cellulose pyrolysis. **Agricultural and Biological Chemistry**, v. 45, n. 2, p. 443-451, 1981.
- SALAH, Sheteiwy Mohamed et al. Seed priming with polyethylene glycol regulating the physiological and molecular mechanism in rice (*Oryza sativa* L.) under nano-ZnO stress. **Scientific Reports**, v. 5, n. 1, p. 14278, 2015.
- SARI, Mustafa Emre et al. Magnetopriming enhance germination and seedling growth parameters of onion and lettuce seeds. **International Journal of Agriculture Environment and Food Sciences**, v. 7, n. 3, p. 468-475, 2023.
- SHABIR, Sumera et al. Deciphering the role of plant-derived smoke solution in ameliorating saline stress and improving physiological, biochemical, and growth responses of wheat. **Journal of Plant Growth Regulation**, v. 41, n. 7, p. 2769-2786, 2022.
- SHAH, Faheem Afzal et al. Karrikin improves osmotic and salt stress tolerance via the regulation of the redox homeostasis in the oil plant *Sapium sebiferum*. **Frontiers in Plant Science**, v. 11, p. 216, 2020.

SILVA, Manoela FF da; SECCO, Ricardo de S.; LOBO, Maria da Graça A. Aspectos ecológicos da vegetação rupestre da Serra dos Carajás, Estado do Pará, Brasil. **Acta amazônica**, v. 26, n. 1-2, p. 17-44, 1996.

SILVA, Patrícia et al. Future projections of fire occurrence in Brazil using EC-Earth climate model. **Revista Brasileira de Meteorologia**, v. 31, n. 3, p. 288-297, 2016.

SILVA, Victor Navarro et al. Seed Priming of *Handroanthus heptaphyllus* for the Restoration of the Mining Fields. **Water, Air, & Soil Pollution**, v. 234, n. 1, p. 31, 2023.

SILVEIRA, Fernando AO et al. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. **Plant and soil**, v. 403, n. 1, p. 129-152, 2016.

SIMPSON, Kimberley J.; ARCHIBALD, Sally; OSBORNE, Colin P. Savanna fire regimes depend on grass trait diversity. **Trends in Ecology & Evolution**, v. 37, n. 9, p. 749-758, 2022.

SINGH, Sarika et al. Plant-derived smoke water and karrikinolide (KAR1) enhance physiological activities, essential oil yield and bioactive constituents of *Mentha arvensis* L. **Frontiers in Plant Science**, v. 14, p. 1129130, 2023.

SINGH, Satendra; KULKARNI, Manoj G.; VAN STADEN, Johannes. Biochemical changes associated with gibberellic acid-like activity of smoke-water, karrikinolide and vermicompost leachate during seedling development of *Phaseolus vulgaris* L. **Seed Science Research**, v. 24, n. 1, p. 63-70, 2014.

SINGH, Shikha; KUMARI, Tanu. Fire and Ecophysiological Responses of Tropical Plants. In: **Ecophysiology of Tropical Plants**. CRC Press, 2023. p. 161-174.

SINGH, Tavisha; BEDI, Seema; SINGH, Rajinder. Effects of Seed Priming on Germinability and Biochemical Parameters of *Praecitrullus Fistulosus* (Stocks) Pangalo. **Bangladesh Journal of Botany**, v. 53, n. 2, p. 217-225, 2024.

SINGLETON, Megan P. et al. Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. **Forest ecology and management**, v. 433, p. 709-719, 2019.

Smolikova, G., Strygina, K., Krylova, E., Leonova, T., Frolov, A., Khlestkina, E.K., & Medvedev, S. (2021). Transition from Seeds to Seedlings: Hormonal and Epigenetic Aspects. *Plants*, 10.

Smolikova, G., Strygina, K., Krylova, E., Vikhorev, A., Bilova, T.E., Frolov, A., Khlestkina, E.K., & Medvedev, S. (2022). Seed-to-Seedling Transition in *Pisum sativum* L.: A Transcriptomic Approach. *Plants*, 11.

Smolikova, Galina and Sergei Medvedev. "Seed-to-Seedling Transition: Novel Aspects." *Plants* 11 (2022): n. pag.

Soós, V., Sebestyén, E., Juhász, A., Light, M. E., Kohout, L., Szalai, G., et al. (2010). Transcriptome analysis of germinating maize kernels exposed to smoke-water and the active compound KAR₁. *BMC Plant Biology*, 10(1), 236.

SOUZA, Jumara Marques; SCHMIDT, Isabel Belloni; CONCEICAO, Abel Augusto. How do fire and harvesting affect the population dynamics of a dominant endemic Velloziaceae species in campo rupestre?. *Flora*, v. 238, p. 225-233, 2018.

STADEN, Johannes Van et al. Smoke as a germination cue. *Plant Species Biology*, v. 15, n. 2, p. 167-178, 2000.

STEINBRECHER, Tina; LEUBNER-METZGER, Gerhard. The biomechanics of seed germination. *Journal of Experimental Botany*, v. 68, n. 4, p. 765-783, 2017.

STURM, Arnd; TANG, Guo-Qing. The sucrose-cleaving enzymes of plants are crucial for development, growth and carbon partitioning. *Trends in plant science*, v. 4, n. 10, p. 401-407, 1999.

SUNMONU, T. O.; KULKARNI, M. G.; VAN STADEN, J. Smoke-water, karrikinolide and gibberellic acid stimulate growth in bean and maize seedlings by efficient starch mobilization and suppression of oxidative stress. *South African Journal of Botany*, v. 102, p. 4-11, 2016.

TEODORO, G. S., Lambers, H., Nascimento, D. L., de Britto Costa, P., Flores-Borges, D. N., Abrahão, A., ... & Oliveira, R. S. (2019). Specialized roots of Velloziaceae weather quartzite rock while mobilizing phosphorus using carboxylates. *Functional Ecology*, 33(5), 762-773.

VAN STADEN, J.; JÄGER, A. K.; STRYDOM, AJPGR. Interaction between a plant-derived smoke extract, light and phytohormones on the germination of light-sensitive lettuce seeds. **Plant Growth Regulation**, v. 17, n. 3, p. 213-218, 1995.

VARELA, Vassiliki et al. Projection of forest fire danger due to climate change in the French Mediterranean region. **Sustainability**, v. 11, n. 16, p. 4284, 2019.

VIEIRA, B. C. et al. Abscisic acid regulates seed germination of *Vellozia* species in response to temperature. **Plant Biology**, v. 19, n. 2, p. 211-216, 2017.

WANG, Peilin et al. Photomorphogenesis in plants: The central role of phytochrome interacting factors (PIFs). **Environmental and Experimental Botany**, v. 194, p. 104704, 2022.

WANG, Weixuan et al. Seed priming with protein hydrolysate promotes seed germination via reserve mobilization, osmolyte accumulation and antioxidant systems under PEG-induced drought stress. **Plant Cell Reports**, v. 41, n. 11, p. 2173-2186, 2022.

Warpeha, K.M., & Montgomery, B.L. (2016). Light and hormone interactions in the seed-to-seedling transition. *Environmental and Experimental Botany*, 121, 56-65.

WATERS, Mark T.; NELSON, David C. Karrikin perception and signalling. **New Phytologist**, v. 237, n. 5, p. 1525-1541, 2023.

WEBER, Hans et al. Selective and powerful stress gene expression in *Arabidopsis* in response to malondialdehyde. **The Plant Journal**, v. 37, n. 6, p. 877-888, 2004.

YAĞCI, Adem; DALER, Selda; KAYA, Ozkan. An Innovative Approach: Alleviating Cadmium Toxicity in Grapevine Seedlings Using Smoke Solution Derived from the Burning of Vineyard Pruning Waste. **Physiologia Plantarum**, v. 176, n. 6, p. e14624, 2024.

YAMAUCHI, Yasuo et al. Malondialdehyde generated from peroxidized linolenic acid causes protein modification in heat-stressed plants. **Plant physiology and biochemistry**, v. 46, n. 8-9, p. 786-793, 2008.

YAN, An; CHEN, Zhong. The control of seed dormancy and germination by temperature, light and nitrate. **The Botanical Review**, v. 86, n. 1, p. 39-75, 2020.

YANG, Tao; LIAN, Yuke; WANG, Chongying. Comparing and contrasting the multiple roles of butenolide plant growth regulators: strigolactones and karrikins in plant development and adaptation to abiotic stresses. **International journal of molecular sciences**, v. 20, n. 24, p. 6270, 2019.

Yemm, E. W. & E. C. Cocking. 1955. The determination of amino acids with ninhydrin. *Analyst*, 80 : 209-213.

ZEMUNIK, Graham et al. High abundance of non-mycorrhizal plant species in severely phosphorus-impooverished Brazilian campos rupestres. **Plant and Soil**, v. 424, p. 255-271, 2018.

ZHANG, Fei et al. Seed priming with polyethylene glycol induces physiological changes in sorghum (*Sorghum bicolor* L. Moench) seedlings under suboptimal soil moisture environments. **Plos one**, v. 10, n. 10, p. e0140620, 2015.

ZIRONDI, Heloiza Lourenço et al. Heat and smoke affect the germination of flammable resprouters: *Vellozia* species in the Cerrado. **Folia Geobotanica**, v. 54, n. 1, p. 65-72, 2019.

ZUPO, Talita et al. Post-fire regeneration strategies in a frequently burned Cerrado community. **Journal of Vegetation Science**, v. 32, n. 1, p. e12968, 2021.